

Researches on Growth and Movement in Plants by Means of the High Magnification Crescograph.

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The auxanometers usually employed for recording longitudinal growth allow a magnification of only 10 or 20 times. The growth of a plant is, however, so slow that it requires several hours to detect the normal rate of growth and its variation under any changed condition. It is, moreover, impossible to maintain the external conditions absolutely constant throughout the experiment; even if this were possible, there would be some autonomous variation of the rate of growth during such lengthy periods. Hence, there must always be some uncertainty in the results obtained by a method which requires long time for observation. The elements of uncertainty can only be eliminated by reducing the period of the experiment to a few minutes, but that would necessitate devising a method of very high magnification and automatic record of the magnified rate of growth.

I attempted to solve this problem by the employment of the optic lever, where an axis carrying a mirror underwent rotation proportional to the growth-elongation. The reflected spot of light magnified the movement of growth from 1000 to 10,000 times. The vertical movement of the spot of light was converted into a horizontal movement by means of a mirror suitably inclined. The excursion of the spot of light was followed by means of a pen on a drum revolving at a known rate; or the record was obtained automatically by photography. Hence a curve was obtained whose ordinate gave growth-movement, and abscissa time.*

Records thus obtained opened out a very extensive field of investigation on growth and its variations under the manifold influences of environment. The photographic method was automatic, but necessitated the discomfort and inconvenience of a dark room; the results, moreover, could not be followed visually. The other method of obtaining the curve of growth by following the excursion of the spot of light with a pen was far more convenient, but the results in this case are likely to be affected by personal error. In order to obviate all these difficulties I devised a direct method, in which the plant by its own autographs exhibits the absolute rate of growth and the induced variations in an extremely short period of time. I propose, in this paper, to give an account of some of the researches which I have been carrying out

* Bose, 'Plant Response,' 1906, p. 421.

by this new method for the last six years; the experiments have been repeated year after year on a variety of plants and with consistent results.

A. THE HIGH MAGNIFICATION CRESCOGRAPH.

1. Method of high magnification.
2. Automatic record of the rate of growth.
3. Experimental adjustments.
4. Determination of latent period and time-relations of response to stimulus.

B. EFFECT OF INDIRECT STIMULATION.

5. Mechanical and electrical response.
6. Effect on growth.

C. TROPIC AND NASTIC MOVEMENTS.

7. General considerations.
8. Tropic curvature with longitudinal transmission of stimulus.
9. Geotropism.
10. Tropic curvature with transverse transmission of stimulus.
11. Mechanotropism; twining of tendrils.
12. Galvanotropism and electrotropism.
13. Theronasty.
14. Positive phototropism.
15. Dia-phototropism and negative phototropism.
16. Radio-thermotropism.
17. Photonasty.

D. RELATION BETWEEN RESPONSE TO STIMULATION OF NON-GROWING AND OF GROWING ORGANS.

18. Similarity of response of growing and non-growing organs.

A. THE HIGH MAGNIFICATION CRESCOGRAPH.

I secured high magnification by means of a compound system of two or more levers. The plant is attached to the short arm of a lever, the long arm of which is attached to the short arm of the second lever. If the magnification by the first lever be m , and that by the second n , then the total magnification would be mn .

1. *Method of High Magnification.*

The practical difficulties met with in carrying out this idea are very numerous. It will be understood that just as the imperceptible movement is highly magnified by the compound system of levers, the various errors and difficulties are likely to be magnified in the same proportion. The principal difficulties met with were due: (1) to the weight of the compound lever, which exerted a great tension on the growing plant; (2) to the yielding of flexible connections by which the plant was attached to the first lever, and the first lever to the second; and (3) to the friction at the fulcrums.

Weight of the Lever.—As the first lever is to exert a pull on the second, it has to be made rigid. The second lever serves as an index, and can therefore be made of fine glass fibre. To secure rigidity of the first lever large cross-section and consequent weight is required, which exerts considerable tension on the plant. Excessive tension greatly modifies growth; even the weight of the index used in self-recording auxanometers is found to retard the normal rate of growth. The weight of the levers introduces an additional difficulty in the increased friction at the fulcrums on account of which there is an obstruction of the free movement of the recording arm of the lever. The conditions essential for overcoming the various difficulties are therefore: (1) construction of a very light lever possessing sufficient rigidity, and (2) arranging the levers in such a way that the tension on the plant may be reduced to any extent, or even eliminated.

I found in "navaldum," an alloy of aluminium, a light material possessing sufficient rigidity. The lever is constructed out of a thin narrow sheet 25 cm. in length. The first lever has, as explained before, to be fairly rigid in order to exert a pull on the second without undergoing any bending; this rigidity is secured by giving the thin narrow plate of the lever a T-shape. The first lever balances, to a certain extent, the second. Finer adjustments are made by means of an adjustable counterpoise B, at the end of the levers. By this means the tension on the plant can be greatly reduced, or a constant tension may be exerted by means of weight T (fig. 1). In my later type of apparatus the plant-connection is made to the right instead of the left side of the first fulcrum. This gives certain practical advantages. The second lever is then made practically to balance the first, only a very slight weight being necessary for exact counterpoise. The reduction of total weight thus secured reduces materially the friction at the fulcrum, with great enhancement of efficiency of the apparatus.

The recording lever has a normal excursion through 8 cm. on the recording surface, which is a very thin sheet of glass 8 x 8 cm., coated with a

thin layer of smoke. As the recording lever is about 40 cm. in length, the curvature in the record is slight, and practically negligible in the middle

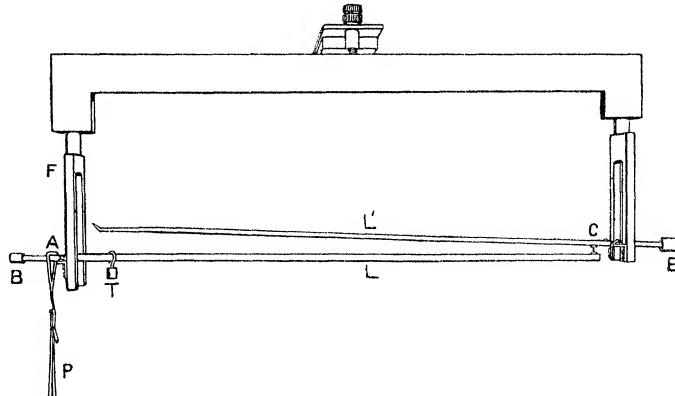


FIG. 1.—Compound lever. P, plant attached to short arm of lever, L ; T, weight exerting tension ; C, connecting link ; L', second lever with bent tip for tracing record. BB, balancing counterpoise ; Fork, F, carrying on its sides two conical agate cups, on which lever rests by two pin-points.

portion through a length of 4 cm. The dimensions given allow a magnification of 10,000. A far more compact apparatus is made with 15 cm. levers. This gives a magnification of 1000.

Connecting Links.—Another puzzling difficulty lay in the fact that the magnification actually obtained was sometimes very different from the calculated value. This unreliability I was able to trace to the defects inherent in the thread-connections at first employed to attach the plant to the first lever and the first lever to the second. These flexible connections were found to undergo variable amounts of elastic yield. Hence it became necessary to use nothing but rigid connections. The plant-attachment, A, of triangular shape is made of a piece of naval-drum ; its knife-edge rests in a notch on the short arm of the lever, L. There are several notches at various distances from the fulcrum. It will be understood how the magnification can be modified by moving A nearer to or further from the fulcrum. The lower end of the attachment is bent in the form of a hook. The end of the leaf of the plant P is doubled on itself and tied. The loop thus formed is then slipped over the hooked end of A.

The link, C, connecting L and L' (fig. 1) consists of a pin pointed at both ends, which rests on two conical agate cups fixed to the upper and lower surfaces respectively of the levers L and L'. This mode of frictionless linking is rigid and allows at the same time perfectly free movement of the levers.

The Fulcrum.—The most serious difficulty was in connection with frictionless support of the axes of the two levers. The horizontal axis was at first supported on jewel bearings, with fine screw adjustment for securing lateral support. Any slight variation from absolute adjustment made the bearing either too loose or too tight, preventing free play of the lever. When perfect adjustment had been secured, the movement of the levers became jerky after a few days. This I afterwards discovered was due to the deposit of invisible particles of dust on the bearings. There were frequent interruptions of work on account of the break of the fine points in the pivot, which have to bear considerable strain in a lateral direction. These difficulties forced me to work out a very perfect and at the same time a much simpler device. The lever now rests on two fine vertical pin-points on conical agate cups carried by the fork F. The axis of the lever passes through the points of support. The friction of support is thus reduced to a minimum and the lever is kept in place under the constant pressure of its own weight. The excursion of the recording end of the lever, which represents magnified movement of growth, was now found to be without jerk and quite uniform.

It is possible to construct a still more sensitive instrument by means of a compound system consisting of *three* levers. There is, however, a limit to the number of levers that may be employed with advantage: for the slight overweight of the last lever becomes multiplied and exerts great tension on the plant, thus interfering with its normal growth.

2. *Automatic Record of the Rate of Growth.*

Another great difficulty in obtaining an accurate record of the curve of growth arises from the friction of contact of the bent tip of the writing lever against the recording surface. This I was able to overcome by an oscillating device in which the contact, instead of being continuous, is made intermittent. The smoked glass plate, G, is made to oscillate to and fro at regular intervals of time, say one second. The bent tip of the recording lever comes periodically in contact with the glass plate during its extreme forward oscillation. The record would thus consist of a series of dots, the distance between successive dots representing magnified growth during a second.

The drawback in connection with the obtaining of a record on the oscillating plate lies in the fact that if the plate approaches the recording point with anything like suddenness, then the stroke on the flexible lever causes an after-oscillation; the multiple dots thus produced spoil the record. In order to overcome this, a special contrivance is necessary, by which the speed of approach of the plate should be gradually reduced to zero at contact with the

recording point. The rate of recession should, on the other hand, continuously increase from zero to maximum. The recording point will in this manner be gently pressed against the glass plate, marking the dot, and then gradually set free. It is only by strict observance of these conditions that the disturbing effect of after-vibration of the lever can be obviated.

This particular contrivance consists of an eccentric rod actuated by a rotating wheel. A cylindrical rod is supported eccentrically, so that semi-rotation of the eccentric causing a pull on the crank K (fig. 2) pushes the

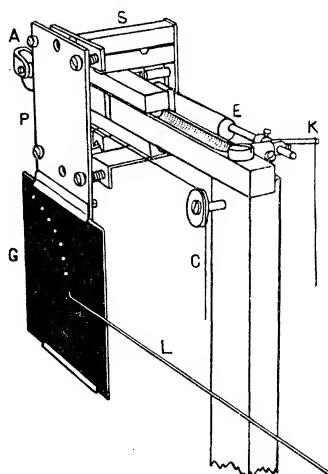


FIG. 2.—Eccentric for oscillation of plate ; K, crank ; S, slide ; P, holder for glass plate G ; A, adjusting screws ; L, recording lever. Clock releases string, C, for lateral movement of the plate.

plate-carrier gradually forward. On the return movement of the eccentric, a light antagonistic spring makes the plate recede. The rate of movement of the crank itself is further regulated by a revolving wheel which is released periodically by clockwork at intervals of 1, 2, 5, 10, or 15 seconds respectively, according to the requirements of the experiment. The complete apparatus is shown in fig. 3.

I used at first a pair of parallel eccentrics, but in the newest type of apparatus with improved to-and-fro sliding arrangement, one eccentric is found to be quite sufficient. A very important condition for success is the securing of perfect smoothness of movement during the oscillation of the plate. A horizontal slide, moving on ball-bearings, carries the vertical plate-holder. The slide is so perfect in action that a puff of air is by itself sufficient to move the free plate-carrier either backward or forward. The plate may thus be maintained in its to-and-fro oscillation with very little expenditure of force, and the power drawn from the wound-up clock is

therefore very small. I have recently been experimenting with an electric oscillating device, which simplifies the matter still further. Electric current flows intermittently through a coil of wire which sucks in a rod of soft iron attached to the plate-carrier. The force required for bringing about the oscillatory movement thus acts directly, without any intervention of the eccentric.

The amplitude of oscillation of the plate is about 3 mm. It is important that the vertical recording plate should be so adjusted that its distance from the recording tip should remain the same during the excursion of the index or during the lateral displacement of the plate moved by clockwork. Failure to secure this makes the dot-marks unequally distinct; in the worst cases some of the dots may even be missing. The difficulty is obviated by accurate adjustment of the plate in a vertical plane by means of regulating screws.

With the particular connection and arrangement of levers the recording tip comes down with growth-elongation. It is perhaps more natural to associate upward growth with an up-curve. The record can, however, be easily reversed by turning over the plate and inspecting the dots from the unsmoked side of the plate.

3. *Experimental Adjustments.*

Adjustment of Tension.—I have explained how the tension exerted on the plant could be rendered negligible. In other cases it may be desirable to apply a definite tension or to increase or decrease it in a quantitative manner. Normally, the levers are so adjusted by suitable counterpoise, as to bring the recording tip to the zero position, which is half-way up the plate. A weight of, say, 1 grm. is now placed on the attachment A (fig. 1) and a weight, T (found by experiment), placed on a fixed notch in L, so as to bring the recording tip once more to zero position. It is clear that when the plant is attached to A, T exerts on it a tension of 1 grm. Various weights are in a similar manner employed to exert tension on the plant from 1 to 10 grm. The tension generally used is about 3 grm.

Determination of the Magnifying Power.—There are two micrometric adjustments, S and S' (fig. 3), one rough and the other fine, by which the plant may be raised or lowered and the recording tip brought to any part of the glass plate. With the connection of the levers shown in fig. 1, the upward growth of the plant lowers the right arm of the lever L, and the recording tip of the second lever L' also moves downwards with the growth of the plant. To determine the magnifying power, a fine black dot is made at the point of attachment of lever and plant, and a particular division of the scale of a microscope-micrometer is focussed to the mark. By means of the micrometer screw, S, a fixed rod attached to the first lever is lowered till

the mark is moved through, say, 1 mm. The magnified movement of the other end of the lever at C is measured on a scale. By careful adjustment

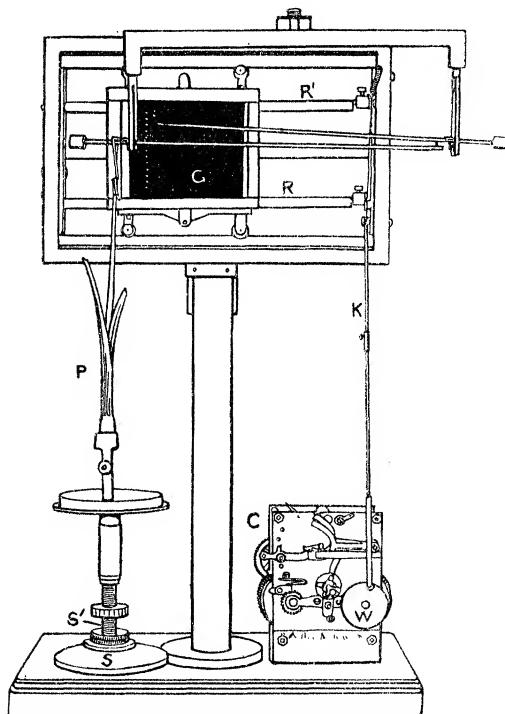


FIG. 3.—Complete apparatus. P, plant; S, S', micrometer screws for raising or lowering the plant; C, clockwork for periodic oscillation of plate; W, rotating wheel.

of the distance of attachment A, from the fulcrum, the magnification of the first lever is made about 100 times. The same procedure is followed to obtain the magnifying power of the second lever. Final adjustments are so made that the actual compound magnification obtained is 10,000 times. In other cases the magnifications employed are 5000, 2000, and 1000.

Experimental Accessories.—The soil in a flower pot is liable to be disturbed by irrigation and the record thus vitiated by physical disturbance. This is obviated by wrapping a piece of cloth round the root imbedded in a small quantity of soil. The lower end of the plant is held securely by the clamp of the plant-holder. In order to subject the plant to the action of gases and vapours, or to variation of temperature, it is enclosed in a cylindrical chamber constructed of a sheet of mica. The chamber is maintained in a humid condition by means of a sponge soaked in water. To study the direct and after-effects of vapours and gases, the vessel V is filled with the given vapour and the second vessel V' with air or water-vapour (fig. 4). The plant-

chamber is filled with a given gas by the working of bellows and the manipulation of the key K; after a given time the gas is replaced by normal air.

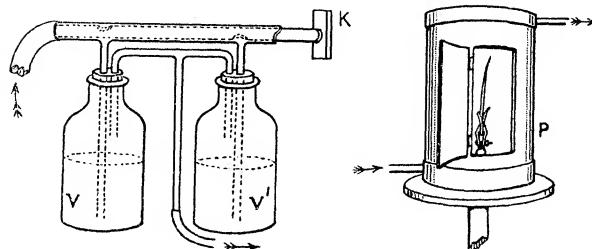


FIG. 4.—P, plant-chamber ; V, V', vessels for introducing into the plant-chamber hot or cold water-vapour, different gases or air, by manipulation of key, K.

For variation of temperature the two vessels are filled, one with hot and the other with cold water. The plant may thus be subjected to a given variation of temperature, by the injection of hot or cold water-vapour into the plant-chamber.

Any quick-growing organ of a plant will be found suitable for experiment. In order to avoid all possible disturbing action of circumnutation, it is preferable to employ either radial organs, such as flower peduncles and the buds of certain flowers, or the limp leaves of various species of grasses and the pistils of flowers. It is also advisable to select specimens in which the growth is uniform. I give below a representative list of various specimens in which, under favourable condition, the rates of growth are of the following order :—

Peduncle of <i>Crocus</i>	0.05	mm. per hour.
(<i>Zephyranthes tubispatha</i> , Herb.)		
Flower bud of <i>Crinum</i>	0.07	„ „
Leaf of grass	1.10	„ „
Pistil of <i>Hibiscus</i> flower	1.20	„ „
Seedling of wheat	1.60	„ „
Seedling of <i>Kysoor</i>	3.00	„ „

A specimen which I found very suitable for experiments on growth is a Cyperaceous plant, *Scirpus Kysoor*, Roxb., locally known as *Kysoor*. The leaves are much stronger than those of wheat and different grasses, and can bear considerable amount of pull without harm. Its rate of growth under favourable condition of season is considerable. Some specimens were found to have grown more than 8 cm. in the course of 24 hours or more than 3 mm. per hour. This was during the rainy season in the month of August, but a month later the rate of growth fell to about 0.8 mm. per hour.

I will now proceed to describe certain typical experiments which will show: (1) the extreme sensibility of the crescograph; (2) its wide applicability to different investigations; and (3) its capability of determining with great precision the time-relations of responsive changes in the rate of growth. In describing these typical cases, I give a detailed account of the experimental methods employed, and thus avoid repetition in describing subsequent experiments.

Expt. 1. Determination of the Absolute Rate of Growth.—I will describe the results of a record on a stationary plate obtained with *Kysoor*. The oscillation-frequency of the plate was once in a second, and the magnification employed was 10,000 times. The magnified growth-movement was so rapid that the record consists of a series of short dashes instead of dots (fig. 5, a).

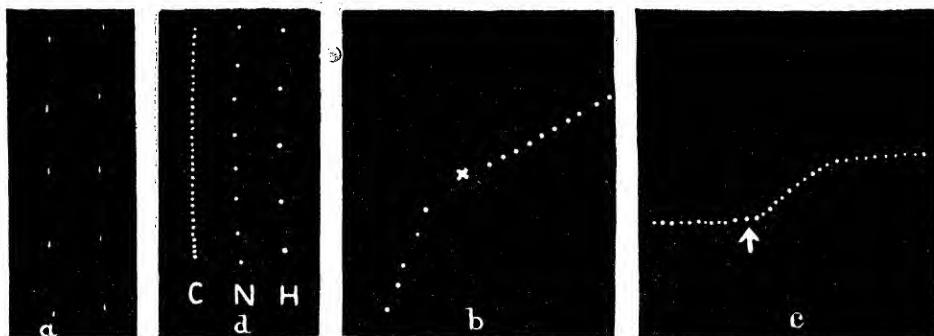


FIG. 5.—Crescographic records. *a*, successive records of growth at intervals of 1 second : $\times 10,000$, with a stationary plate. Effect of temperature: *d*, N, normal rate of growth ; C, retarded rate under cold ; H, enhanced rate under warmth ; *b*, record on moving plate, where diminished slope of curve denotes retarded rate under cold ; *c*, horizontal record showing absence of growth in dead branch ; physical expansion on application of warmth at arrow followed by horizontal record on attainment of steady temperature. $\times 2000$.

For securing regularity in the rate of growth, it is advisable that the plant should be kept in uniform darkness or in uniformly diffused light. So sensitive is the method of record that it shows a change of growth-rate due to the slight increase of illumination by the opening of an additional window. One-sided light, moreover, gives rise to disturbing phototropic curvature. With the precautions described, the growth-rate in vigorous specimens is found to be very uniform.

After the completion of the first vertical series, the recording plate was moved 1 cm. to the left; the tip of the recorder was brought once more to the top by means of the fine screw adjustment S (fig. 3), and the record taken once more after an interval of 15 minutes. The magnified record for

4 seconds is 38 mm. in the first record. It is precisely the same in the record taken 15 minutes later. The successive growth-elongations at intervals of 1 second are practically the same throughout, being 9.5 mm. This uniformity in the spacings demonstrates not only the regularity of growth under constant conditions, but also the reliability and perfection of the apparatus. It also shows that by keeping the external conditions constant, the normal growth-rate could be maintained uniform for at least 15 minutes. As the magnified growth is nearly 1 cm. per minute, and as it is quite easy to measure 0.5 mm., the crescograph enables us to record a length of 0.00005 mm., that is to say, the sixteenth part of a wave of red light. The absolute rate of growth, moreover, can be determined in a period as short as 0.05 second. These facts will give us some idea of the enormous possibilities of the crescograph for future investigation.

As the period of the experiment is very greatly shortened by the method of high magnification, I shall, in the determination of the absolute rate of growth, adopt a second as the unit of time and μ or micron as the unit of length—the micron being 0.000001 metre, or 0.001 mm.

If m be the magnifying power of the compound lever, and l the average distance between successive dots in millimetres at intervals of t seconds, then

$$\text{rate of growth} = \frac{1}{mt} \times 10^3 \mu \text{ per sec.}$$

In the record given $l = 9.5$ mm., $m = 10,000$, $t = 1$ second.

Hence rate of growth

$$= \frac{9.5}{10,000} \times 10^3 \mu \text{ per sec.} = 0.95 \mu \text{ per sec.}$$

Expt. 2. Precaution against Physical Disturbances.—There may be some misgiving about the employment of such high magnification; it may be thought that the accuracy of the record might be vitiated by physical disturbance, such as vibration. In physical experimentation far greater difficulties have been overcome, and the problem of securing freedom from vibration is not at all formidable. The whole apparatus need only be placed on a heavy bracket screwed on the wall to ensure against mechanical disturbance. To what extent this has been realised will be found from the inspection of the first part of the record in fig. 5, c, taken on a moving plate. A thin dead twig was substituted for the growing plant, and a perfectly horizontal record not only demonstrated the absence of growth-movement but also of all disturbance. There is also another element of physical change, against which precautions have to be taken in experiments on variation of

the rate of growth with rising temperature. In order to determine its character and extent, a record was taken, with the dead twig, of the effect of raising the temperature of the plant-chamber through 10° . The record, with a magnification of 2000, shows that there was an expansion during the rise of the temperature, after which there was a cessation of physical movement, the record becoming once more horizontal. The obvious precaution to be taken in such a case is to wait for several minutes for the attainment of steady temperature. The movement caused by physical change abates in a short time, whereas the change of rate of growth brought about by physiological reaction is persistent.

Having demonstrated the extreme sensitiveness and reliability of the apparatus in quantitative determinations, I proceed to show its wide applicability for various researches relating to the influence of external agencies in modification of growth. For this two different methods are employed. In the first, the records are taken on a stationary plate; the first in the series gives the normal rate; the second is the record taken under the given changed condition. The increase or diminution of the space between successive dots in the two records at once demonstrates the stimulating or depressing nature of the changed condition. In the second method, the record is taken on a plate moving at a uniform rate by clockwork. A curve is thus obtained, the ordinate representing growth-elongation and the abscissa the time. The increment of length divided by the increment of time gives the absolute value of growth at any part of the curve. As long as growth is uniform, so long the slope of the curve remains constant. If a stimulating agency enhances the rate of growth, there is an immediate flexure in the curve. A depressing agent lessens the slope of the curve.

Expt. 3.—I will now give a few typical examples of the employment of the crescograph for the investigation of growth; the first example I shall take is the demonstration of the influence of temperature.

Stationary Method.—Fig. 5, *d*, gives records taken on a stationary plate. The specimen used was *Kysoor*; the crescograph magnification was 2000, and the successive dots at intervals of 5 secs. The middle series, *N*, was at the temperature of the room. The next, *C*, was obtained with the temperature lowered by a few degrees. Finally, *H* was taken when the plant-chamber was warmed. It will be seen how under cooling the spaces between successive dots have become shortened, showing the diminished rate of growth. Warming, on the other hand, caused a lengthening of the spaces between successive dots, thus demonstrating an enhancement of the rate of growth.

Calculating from the data obtained from the figure, we find :

Absolute value of normal rate	0.457 μ per sec.
Diminished rate under cold	0.101 " "
Enhanced rate under warmth	0.737 " "

Moving Plate Method.—Another experiment was carried out with a different specimen of *Kysoor*, the record being taken on a moving plate (fig. 5, b). The left part of the curve here represents the normal rate of growth. The plant was then subjected to moderate cooling, and the subsequent curve with its diminished slope denotes the depression of growth.

4. Determination of Latent Period and Time-Relations of Response to Stimulus.

Expt. 4.—In the determination of time-relations of responsive change in growth under external stimulus, I take the typical case of the effect of electrical shock of one second's duration from a secondary coil. Two electrodes were applied, one above and the other below the growing region of a bud of *Crinum*. The record was taken on a moving plate, magnification employed being 2000, and successive dots made at intervals of 2 seconds. It was a matter of surprise to me to find that the growth of the plant was affected by an intensity of stimulus far below the limit of our own perception. For convenience I shall designate the intensity of electric shock that is barely perceptible to us, as the unit shock. When an intensity of 0.25 unit was applied to the growing organ, it responded by a retardation of the rate of growth. As regards the relative sensibility of plant and animal, I may say that the leaf of *Mimosa pudica*, in a favourable condition, responds to an electric stimulus which is one-tenth the minimum intensity that causes perception in a human being.*

Inspection of fig. 6, a, shows that a flexure is induced in the curve in response to stimulus, the flattening of the curve denoting retardation of growth. The latent period in this case was 6 seconds. The normal rate was found restored after a rest of 5 minutes. The intensity of shock was next raised from 0.25 unit to 1 unit. The second record shows that the latent period was reduced to 4 seconds, and a relatively greater retardation of growth was induced by the action of the stronger stimulus. The recovery of the normal rate was effected after the longer period of 10 minutes. I took one more record, the stimulus being 3 units. The latent period was now reduced to 1 second, and the induced retardation was so great as to effect a temporary arrest of growth, after which there was a slow recovery.

Expt. 5.—As a further example of the capability of the crescograph, I will

* Bose, 'Irritability of Plants,' 1913, p. 50.

give the record of a single pulse of growth obtained with the peduncle of *Crocus* (fig. 6, *b*). The magnification employed was 10,000, the successive dots

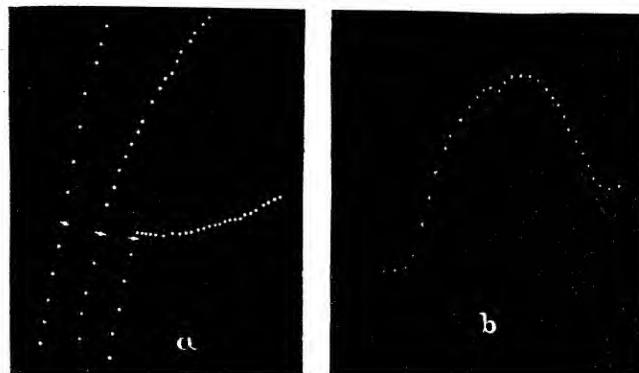


FIG. 6.—*a*, time-relations of response of growing bud of *Crinum* to electric stimulus of increasing intensity applied at the short lines; *b*, record of a single growth-pulse of *Crocus*.

being at intervals of 1 second. It will be seen that the growth-pulse commences with a sudden elongation, the maximum rate being 0.4μ per second. The pulse exhausts itself in 15 seconds, after which there is a partial recovery in the course of 13 seconds. The period of the complete pulse is, therefore, 28 seconds. The resultant growth in each pulse is, therefore, the difference between elongation and recovery. Had a highly magnifying arrangement not been used, the resulting rate would have appeared continuous. In other specimens, owing probably to greater frequency of pulsation and co-operation of numerous elements in growth, the rate appears to be practically uniform.

Table I.—Time-relations of Growth-variation under Electric Shock.
(*Crinum*.)

Intensity of stimulus.	Latent period.	Normal rate.	Retarded rate.
0.25 unit	6 seconds	0.62μ per sec.	0.49μ per sec.
1 unit	4 seconds	0.62 " "	0.25 " "
3 units	1 second	0.62 " "	Temporary arrest of growth.

It is thus found that growth in plants is affected by an intensity of stimulus which is below human perception; that with increasing stimulus the latent period is diminished and the period of recovery increased; that the induced retardation of growth increases continuously with the stimulus till at a critical value there is a temporary arrest of growth.

B. EFFECT OF INDIRECT STIMULATION.

Having ascertained that the direct application of stimulus gives rise in different organs to contraction, diminution of turgor, fall of motile leaf, electromotive change of galvanometric negativity, and retardation of the rate of growth, I proceeded to inquire whether indirect stimulus (that is to say application of stimulus at some distance from the responding organ) gives rise to an effect different from that of direct application.

5. Mechanical and Electrical Response.

In experimenting with various sensitive plants like *Mimosa*, *Averrhoa*, and with ordinary plants like *Artocarpus*, I found that indirect stimulation gives rise to a positive or erectile response of the responding leaf or leaflet (indicative of an increase of turgor), often followed by the normal negative

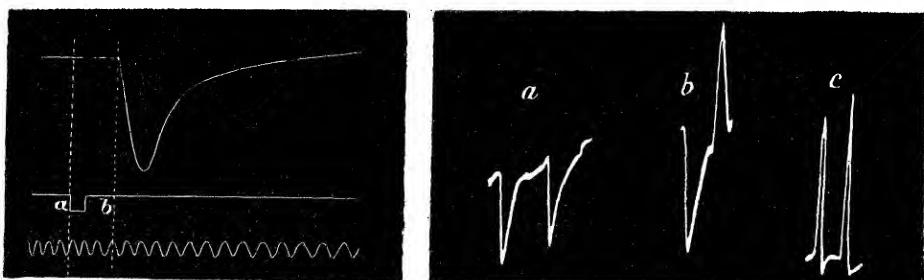


FIG. 7.—Mechanical and electrical response to indirect stimulation. Left, positive response of *Mimosa* : *a*, moment of application of stimulus ; *b*, time-tracings of five vibrations per second. Right, *a*, positive ; *b*, diphasic ; and *c*, negative, electric response of *Musa*.

response ; the interval between the two varies in different cases from a fraction of a second to 30 seconds or more. A probable explanation of the dual impulse is that stimulation causes a local contraction, with expulsion of water from the cells. The positive hydraulic impulse travels quickly. The interval of time that elapses between the application of stimulus and the erectile response of the responding leaf depends on the distance of the point of application and the character of the transmitting tissue ; it varies in different cases from 0.6 second to about 40 seconds. The positive is followed by a slower wave of protoplasmic excitation, which causes the excitatory fall. The velocity of this excitatory impulse is about 30 mm. per second in the petiole of *Mimosa*, and about 3 mm. per second in *Biophytum*. The positive followed by the negative thus gives rise to a diphasic response. The excitatory impulse is much enfeebled during transit ; the negative impulse may fail to reach the responding organ if the stimulus be feeble, or if the

intervening distance be long or semi-conducting. Hence moderate stimulus applied at a distance gives rise only to positive response; direct application of strong stimulus gives rise, on the other hand, to the normal negative. By employing the electric method of investigation, I have obtained with ordinary tissues the positive, the diphasic, and the negative electric response, in correspondence with the responses given by a motile organ (fig. 7).* The mechanics of propagation of the positive and the negative impulse are different. It is therefore necessary to distinguish the quick *transmission* of the hydro-positive impulse from the slow *conduction* of the negative impulse due to the propagation of excitatory protoplasmic change.

6. Effect of Indirect Stimulation on Growth.

I will now describe certain remarkable phenomena connected with growth, the discovery of which was due to the clue obtained from the characteristic response to indirect stimulation that has just been described. I may say here, in anticipation, that the results of experiments which I have carried out on growth-variation under indirect stimulation are precisely parallel to those obtained with non-growing organs. The effect induced by feeble stimulus applied at a distance from the growing region is a positive variation or acceleration of growth, which becomes negative, *i.e.*, retardation of growth, when the stimulus is applied at the responding region of growth; under intermediate conditions, the growth-variation is diphasic, a positive acceleration followed by a negative retardation.

Expt. 6.—Out of these three cases I shall give a detailed account of an experiment relating to the positive variation of growth under moderate indirect stimulation, since this particular case may have some important theoretical significance. I took for experiment a growing bud of *Crinum* and determined the region of its growth activity; lower down a region was found where the growth had already passed its maximum, and may therefore be regarded as an indifferent region. I applied two electrodes on this indifferent region, about 1 cm. below the region of growth. On applying a moderate electric stimulus of short duration, the response was an acceleration of growth which persisted for nearly a minute, after which there was a resumption of the normal rate of growth. In this particular case the interval of time between the application of stimulus and the responsive acceleration of growth was 12 seconds. The interval varied in different cases from 1 second to about 20 seconds, depending on the intervening distance between the point of application of stimulus and the responding region of

* Cf. 'Plant Response,' p. 512; 'Comparative Electrophysiology,' p. 62; 'Irritability of Plants,' p. 176.

growth. I also give a record (fig. 8), which shows in an identical specimen (1) an acceleration of growth under indirect, and (2) a retardation of growth under direct stimulation.

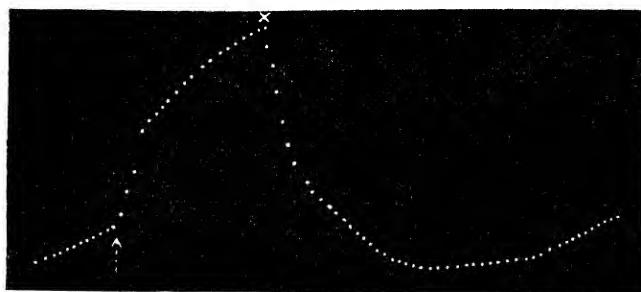


FIG. 8.—Effect of indirect and direct stimulation on growth. (↑) shows application of indirect stimulus with consequent acceleration of growth: application of direct stimulus at (X) induces contraction and subsequent retardation of rate of growth.

Table II.—Accelerating Effect of Indirect Stimulation (*Crinum*).

Specimen.	Rate of growth.		
I	Normal	0.21 μ per sec.
	After indirect stimulation	3.26 " "
II	Normal	0.25 " "
	After indirect stimulation	0.3 " "

From the above results it will be seen that the effect of stimulus is modified by its point of application.

Hence we arrive at the following laws of direct and indirect stimulation*:

1. *Direct Stimulation*—

The effect is contraction, diminution of turgor, negative mechanical and electrical response, negative variation (retardation) of the rate of growth.

2. *Indirect Stimulation*—

(a) The effect of feeble stimulus is expansion, increase of turgor, positive mechanical and electrical response, positive variation (acceleration) of rate of growth.

(b) The effect of prolonged application of stimulus of moderate intensity is a diphasic response, positive mechanical or electrical response followed by the negative; an acceleration, followed by a retardation of growth. If the intervening tissue be highly conducting, the transient positive effect becomes masked by the predominant negative.

* Cf. 'Plant Response,' p. 535; 'Comparative Electro-physiology,' p. 64; 'Irritability of Plants,' p. 196.

It will presently be shown how these fundamental effects of direct and indirect stimulations are instrumental in bringing about various tropic curvatures.

C. TROPIC AND NASTIC MOVEMENTS.

The diverse movements induced by external stimulus in different organs of plants are extremely varied and complicated; the forces in operation are manifold—the influence of changing temperature, the stimulus of contact, of electric current, of gravity, and of light visible and invisible. They act on organs which exhibit all degrees of physiological differentiation, from the radial to the dorsiventral. Stimulus may act on one side or on all sides of the organ. The response may or may not change with the mode of stimulation. In the curving tendril under stimulus of unilateral contact, Fitting finds a pronounced acceleration of growth on the convex side. "Although the exact mode of production of these changes is uncertain, they are undoubtedly the result of the contact stimulus."^{*} Far more complicated are the effects induced by light. Under unilateral stimulation of increasing intensity, a radial organ exhibits a positive, a dia-phototropic and finally a negative response. Strong sunlight brings about para-phototropic or midday sleep movement, by which the apices of leaves or leaflets turn towards or away from the source of illumination. The teleological argument advanced, that in this position the plant is protected from excessive transpiration, does not hold good universally; for under the same reaction the leaflets of *Cassia montana* assume positions by which the plant risks fatal loss of water. In *Averrhoa Carambola* the movement is downwards, whichever side is illuminated with strong light; in *Mimosa* leaflet the movement, under similar circumstances, is precisely in the opposite direction. The photonastic movement, apparently independent of the directive action of light, has come to be regarded as a phenomenon totally unrelated to phototropic reaction, and due to a different kind of irritability and a different mode of response. So very anomalous are these various effects that Pfeffer, after showing the inadequacy of various theories that have been advanced, came to the conclusion that "the precise character of the stimulatory action of light has yet to be determined. . . . When we say that an organ curves towards a source of illumination because of its phototropic irritability, we are simply expressing an ascertained fact in a conveniently abbreviated form, without explaining why such curvature is possible or how it is produced."[†]

* Pfeffer, 'Physiology,' vol. 3, p. 58.

† Pfeffer, 'Physiology,' vol. 2, p. 74.

7. *General Considerations.*

The contradictory nature of the various responses is, however, not real; the apparent anomaly lies in the fact that two distinct fundamental reactions to stimulus had hitherto remained undiscovered. The innumerable variations in the resultant response is due to the summation of the effects of two fluctuating factors; it is therefore most important to have the means of tracing the continuous change in the response brought about by the two elements which are sometimes in accord and at other times in conflict. The autograph of the plant itself giving a history of the change in response and its time-relations is therefore decisive in explanation of the various anomalies in plant-movements, as against the various tentative theories that have been put forward. The analysis of the resultant effect thus rendered possible casts new light on responsive characteristics of various organs, such as the localisation of the sensory zone in *Avena*, the illusive difference between tropic and nastic movement, and many other anomalies which are more apparent than real. Limitation of space compels me to confine myself to the consideration of some important and typical reactions which will give clue for the explanation of others.

All the tropic movements under unilateral stimulus find their explanation from the above laws of direct and indirect stimulation that have been established for all modes of excitation. We have henceforth to deal with two classes of effects, due to longitudinal and transverse transmission respectively. In the former case the transmitted stimulus will cause an expansion higher up on the same side to which the stimulus is applied; the result will be an induced convexity, a movement away from stimulus, *i.e.*, a negative curvature. In the case of transverse transmission, the direct effect on the proximal side will be a contraction, and on the opposite side an expansion. When the stimulus is feeble, or when the tissue is a non-conductor of excitation, the first positive will remain as the final effect. But in other cases, conduction of excitation in a transverse direction will bring about a neutralisation or even a reversal into negative. These theoretical deductions I have put to the test of experiment.

8. *Tropic Curvature with Longitudinal Transmission of Stimulus.*

Expt. 7.—I have already explained how thermal radiation is almost as effective in inducing contraction and retardation of growth as the more refrangible rays of the spectrum. The thermal radiation is produced by the heating of a platinum spiral, short of incandescence, by the passage of an electric current. The intensity of radiation is easily varied by adjustment of

the current by means of a rheostat. The experimental subject was a flower-bud of growing *Crinum*. It was held by a clamp, a little below the region of growth. Stimulus was applied below the clamp so that the transmitted effect had to pass through the securely held tissue. A feeble stimulus was applied on one side, at the indifferent point about 3 cm. below the region of growth. The indirect stimulus reached the region of growth on the same side, bringing about an acceleration of growth with expansion and convexity, the resulting movement being negative or away from the stimulus. The latent period was 10 seconds, and maximum negative movement was completed in the further course of 10 seconds, after which there was a recovery in the course of 75 seconds. A stronger stimulus gave a larger response; but when the intensity was raised still higher, the hydro-positive was overtaken by the excitatory negative impulse within 15 seconds of the commencement of the positive response; the convex was then succeeded by the concave curvature (fig. 9). I have obtained similar negative and positive curvatures

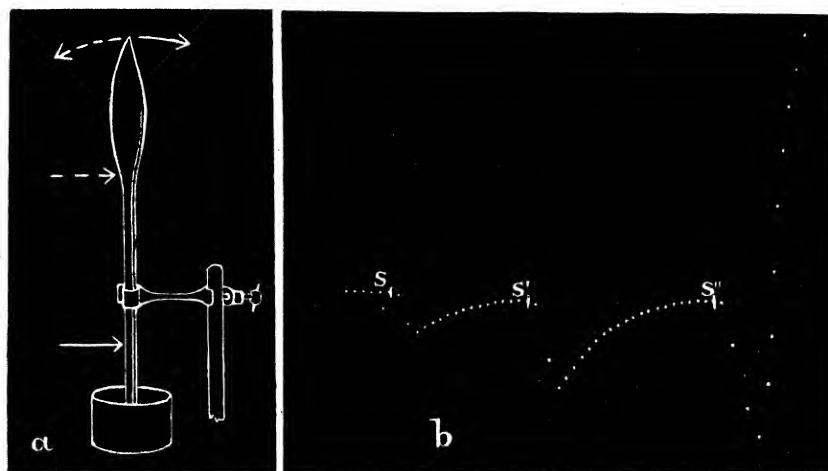


FIG. 9.—Effect of indirect stimulation on growth curvature. *a*, diagrammatic representation: continuous arrow represents indirect stimulation; curved arrow the induced negative curvature; dotted arrow indicates direct application of stimulus; and dotted curve the positive curvature. *b*, indirect stimulation of moderate intensity: S , S' induced negative tropic effect (movement away from stimulated side); stronger stimulus S'' gave rise to negative followed by positive. (*Crinum*.)

with other plant-organs under various forms of stimuli. Thus the indirect effect of continuous application of light of feeble intensity was to increase negative curvature in a stem of *Dregea volubilis*. Direct application of light on the region of growth gave, on the other hand, a positive curvature.

Thus, while the direct effect of unilateral stimulation is to induce a positive

curvature, its longitudinal transmission has the indirect effect of inducing a negative curvature.

9. *Geotropism.*

No phenomenon of tropic response is so inexplicable as the opposite effects of stimulus of gravity on the root and the shoot. The experiment that has just been described will, I think, offer an explanation of these diametrically opposite effects. In the root the stimulus is received at the tip and transmitted to the region of growth at some distance; stimulation here is therefore indirect. In contrast with this is the fact that the growing region of the shoot is both sensitive and responsive. Hence the stimulation in this case is direct. As the effects of direct and indirect stimulation on growth are antithetic, the responses of shoot and root to the direct and indirect actions of stimulus must be of opposite signs.

I have carried out other experiments for determining the effects of direct and indirect stimulation on the root itself. Unilateral stimulation of the tip* by thermal radiation induced a negative curvature, while direct stimulation of the growing region brought about a positive curvature.†

These results indicate that there is no necessity for postulating two different irritabilities for the shoot and the root, since tissues in general exhibit positive or negative curvature accordingly as stimulation is direct or indirect.

10. *Tropic Curvature with Transverse Transmission of Stimulus.*

We have next to consider a very large class of phenomena arising out of the direct stimulation of one side, and its transversely transmitted effect on the opposite site. The unilateral stimuli to which the plant is naturally exposed are those of contact, of light, and of thermal radiation. There is besides the stimulation of the electric current. I shall presently show that these tropic curvatures are determined by the definite effects of direct and indirect stimulations. The twining of tendrils by unilateral contact will be taken first, as presenting fewest complications.

11. *Mechanotropism; Twining of Tendrils.*

In experiments on the effect of mechanical friction on growth, I have found that its direct effect is an incipient contraction and retardation of growth; the incipient contraction culminates in an actual contraction under

* Darwin's experiments on the curvature brought about by unilateral contact or injury of the root-tip show that other stimuli induce an effect similar to that of gravitation.

† For results of further investigation on the subject *cf.* 'Plant Response,' p. 537.

stronger stimulation. Unilateral application of stimulus will bring about a contraction of the proximal side due to the direct effect of stimulation, and an expansion on the distal side due to indirect effect.

Expt. 8. Effect of Diffuse Mechanical Stimulation on the Growth of Tendril.—I took a growing tendril of *Cucurbita*, and, after obtaining record of its normal rate of growth, subjected it to feeble mechanical stimulation by rubbing its different sides. The immediate effect was a retardation from the normal rate of $0.44\ \mu$ per second to $0.20\ \mu$ per second. The tendril recovered its normal rate of growth after the feeble stimulation; in fact, the effect, after 15 minutes, was even a slight acceleration above the normal, the growth rate being $0.59\ \mu$ per second. The contraction of the directly excited side and the expansion due to indirect stimulation of the distal side will give an explanation of Fitting's observation* that in a unilaterally stimulated tendril there is (1) an acceleration of growth on the convex side, and (2) a contraction on the concave side. Fitting noticed that the tendril became straightened by the active renewal of growth on the excited side.

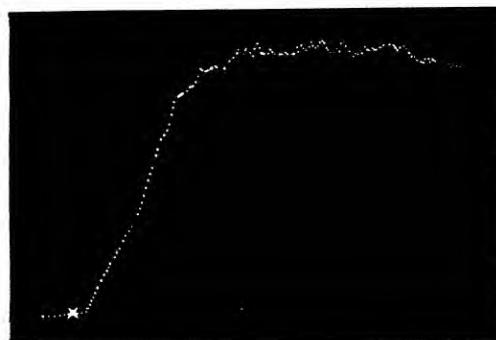


FIG. 10.—Positive curvature of tendril of *Cucurbita* under unilateral stimulus of contact at x.

I give here a record obtained with a single recording lever (magnification 50 times), showing the response to short unilateral contact in a tendril of *Cucurbita*. Positive curvature was induced in about 15 seconds and attained its climax in $2\frac{1}{2}$ minutes, after which the tendril slowly commenced its recovery, which was completed in 12 minutes (fig. 10). Feeble stimulation is attended by a recovery within a moderate period of time. Under strong stimulation the curvature becomes more persistent.

12. Galvanotropism and Electrotropism.

I have demonstrated the retarding effect of the cathode and the accelerating effect of the anode on growth. Unilateral application of anode

* Pfeffer, *ibid.*, vol. 3, p. 57.

or cathode will thus bring about appropriate curvatures. The galvanotropic effect may also be demonstrated by the pulvini of different plants such as those of *Erythrina indica*. One electrode is applied on one half of the pulvinus, say the upper half, the second electrode being applied on the stem. On making the pulvinus cathode, a curvature is produced, due to induced contraction and concavity. Reversing the current and making the pulvinus anode causes an opposite curvature due to induced expansion and convexity. An intensity of current above the critical here reverses expansion into contraction.

Expt. 9.—For obtaining electrotropic response I took a growing bud of *Crinum*, and applied two electrodes on one side of the organ in the growing region. The electrodes were two pins thrust one above the other 1 cm. apart. The effect of mechanical irritation was allowed to pass away. Application of induction-shock of moderate intensity to one flank of the organ gave rise to a positive curvature, the side directly excited becoming concave; there was a recovery after a period of rest.

13. *Thermonasty.*

In the well-known instance of the *Crocus* flower the effect of rise of temperature is to bring about a relatively quicker rate of growth on one side of the anisotropic organ. This causes the movement of opening; fall of temperature induces the reverse effect of closing.

Expt. 10.—I give below records of the effect of rise and fall of temperature. Some specimens were found extraordinarily sensitive, and the following records give the opposite reactions due to alternate introduction of puffs of cold and warm air. The rise of temperature was so slight that a mercury thermometer did not exhibit any change. Yet the effects of such slight variation of temperature gave rise to marked responses of opposite signs. I

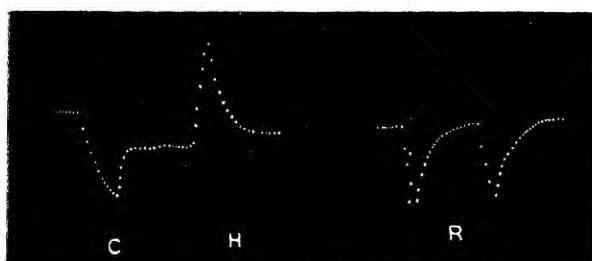


FIG. 11.—Thermonastic and radionastic responses of petal of *Crocus*. C, closing movement due to cooling, and H, opening movement due to warming; R, closing movement due to heat-radiation. Note opposite responses to thermal and radiation action of heat.

here insist once more on the two opposite effects of heat, the *thermal* effect which induces an acceleration and the *radiation* effect which causes a retardation of growth. In order to demonstrate this, I subjected this flower to thermal radiation acting from all sides. The result is a movement which is of opposite sign to the effect of rising temperature (fig. 11).

14. Positive Phototropism.

In the study of the responsive curvature induced by unilateral action of light, we have to deal with the joint effects of the contraction of the proximal and the expansion of the opposite side, which would, under normal conditions, give rise to a positive curvature.

By following the electric mode of investigation I have obtained independent corroboration of the characteristic effects of direct and indirect stimulation on the proximal and opposite sides.* The following Table gives the responsive effects induced in pulvini and in growing tissues which act as pulvinoids:—

Table III.—Showing Responsive Effects Common to Pulvini and Growing Organs under Unilateral Stimulation.

Effect of direct stimulation on proximal side.	Effect of indirect stimulation on distal side.
Diminution of turgor Galvanometric negativity Contraction and concavity	Increase of turgor. Galvanometric positivity. Expansion and convexity.
When stimulus is strong or long continued, the true excitatory effect is conducted to the distal side neutralising or reversing the first response.	

When a radial organ is subjected to the unilateral action of light, it exhibits a positive curvature. Fig. 12 gives the positive response of the stem of *Dregea volubilis* to light of short duration from an arc-lamp; the recovery on cessation of light was complete. When the stimulation was stronger, and continued for a longer time, the curvature was greater, and the after-effect was more persistent. The positive curvature does not undergo any modification in the case of thick organs with feeble transverse conductivity, for neutralisation can only take place by the conduction of excitation to the opposite side.

I have said that the normal positive curvature was brought about by the contraction of the proximal and the expansion of the opposite side. I made

* 'Plant Response,' p. 515.

a surmise that the expansion of the opposite side, due to indirect stimulation, was brought about by an induced increase of turgor.

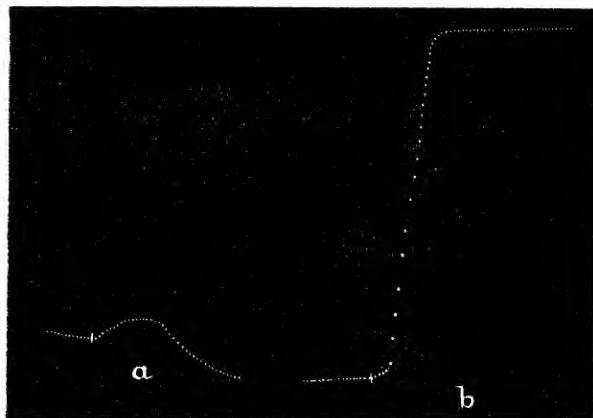


FIG. 12.—*a*, positive phototropic response and recovery from moderate stimulation ; *b*, persistent positive curvature under stronger stimulation. (*Dregea*.)

Expt. 11.—It would, undoubtedly, be a matter of great theoretical interest if the induction of enhanced turgor on the distal side (by the action of stimulus at the proximal side) could be demonstrated by some experiment of a convincing character. I have explained elsewhere how enhanced turgor brought about by increased internal hydrostatic pressure caused an erection of the *Mimosa* leaf, a diminution of turgor causing its fall.* I now took a *Mimosa* plant and applied a narrow circular beam of light from a small arc lamp at a point on the stem diametrically opposite to the motile leaf which was to serve as the indicator of induced variation of turgor under the unilateral action of light. That the indirect stimulation caused an enhancement of turgor of the opposite side was soon demonstrated by the erectile movement of the leaf. This positive movement was initiated 20 seconds after the application of stimulus, thus affording a proof, which appears conclusive, of the induction of an increased turgor as the effect of indirect stimulation. When the stimulation is moderate and of short duration, the response is only positive. But when the stimulation is continued, the slow excitatory impulse is conducted to the distal side with immediate fall of the leaf (fig. 13). It was stated that conduction of excitation in a transverse direction would prove very much slower than in the longitudinal direction. In the present case the time taken for conduction across the stem 2 mm. in diameter was 200 seconds, giving a velocity of $\frac{1}{100}$ mm. per second. The velocity

* 'Plant Response,' p. 46.

along the stem varies in different cases, from one to several millimetres per second. Transverse conductivity is thus about a hundredth of the longitudinal conductivity.

Expt. 12.—I next give an account of experiments on the effect of unilateral

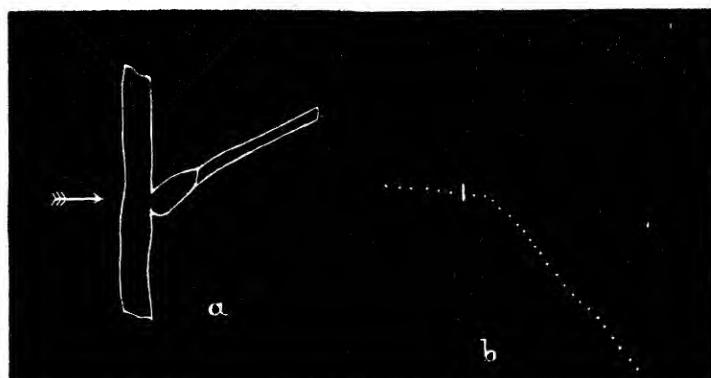


FIG. 13.—Increased turgor due to indirect stimulation, inducing erection of *Mimosa* leaf : *a*, diagram of experiment ; *b*, erectile response (shown by down-curve) followed by rapid fall (up-curve) due to transverse conduction of true excitation.

stimulus of light on the pulvinus of *Mimosa*. The results will be found to be of much theoretical importance, since this single experiment will give an insight into all possible types of phototropic response. I must first remove the general misapprehension that it is the lower half of the pulvinus that is alone excitable. By careful amputation of the lower half I have been able to show that the upper half is also excitable and contracts under electrical stimulation, lifting the leaf. The responsive movement was relatively slower, and the excitability was found to be about one-eightieth that of the lower half.

In my present experiment a beam of light from a small arc-lamp was thrown on the upper half of the pulvinus. After a latent period of 5 seconds, a positive curvature was initiated by the contraction of the upper and expansion of the lower side of the organ. A series of *positive* responses may thus be obtained under stimuli of short duration. But under continued action of light the excitatory impulse reaches the lower half of the organ, causing a rapid fall of the leaf, thus constituting a *negative* response (fig. 14). The thickness of the pulvinus was 1.5 mm. The distance to be traversed to reach the lower half would be about 0.75 mm.; the time taken by the excitatory impulse to traverse this distance was found to vary in different cases from 50 to 80 seconds. The transverse velocity is thus about $\frac{1}{80}$ mm. per second.

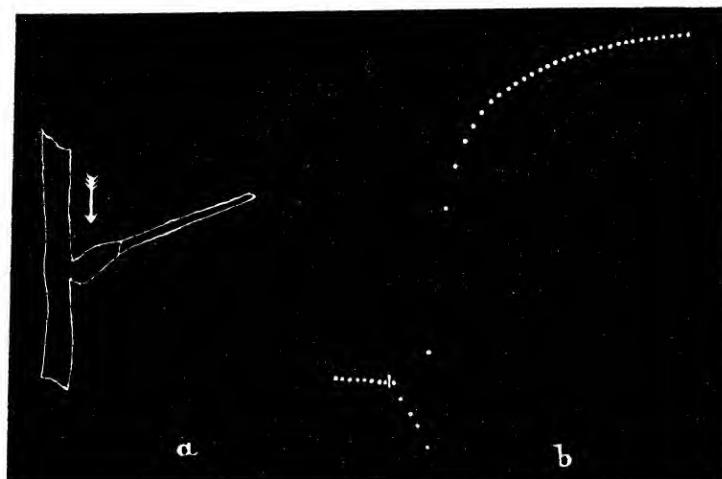


FIG. 14.—Record of effect of continuous application of light on upper half of pulvinus of *Mimosa* leaf. Note erectile response (positive curvature) followed by neutralisation and pronounced reversal into negative due to transverse conduction of excitation. (Up-movement shown by down-curve and *vice versa*.)

Turning to the main experiment, we find that:—

(1) As a result of the action of light on the upper surface, there was a positive phototropic effect which lasted for 50 seconds.

(2) Owing to the internal conduction of excitation, the positive effect underwent an increasing neutralisation on account of the excitatory contraction of the opposite side. This neutralisation depends on four factors: (a) the intensity of the stimulus, (b) the conductivity of the organ in a transverse direction, (c) the thickness of the intervening tissue, and (d) the relative excitability of the opposite as compared with the proximal side. The extent of positive curvature will also depend on the pliability of the organ.

(3) Since the organ exhibits pronounced physiological anisotropy, and the opposite side is far more excitable than the proximal, the internally diffused stimulus brings about a greater contraction of the opposite side. The positive phototropic curvature becomes reversed to a very pronounced negative. The effect of the internally diffused stimulus is thus the same as that of external diffuse stimulation.

(4) When the stimulus is applied on the more excitable side of the organ—in this case the lower half—the result is a predominant contraction of that half; this cannot be neutralised by the excitation conducted to the feebly excitable upper half. As the curvature is towards the stimulus, the phototropic effect will appear to be positive.

Hence, unilateral stimulation of an anisotropic organ will appear to give different results depending on the particular flank that is excited. Stimulation of the less excitable side will give the sequence of positive, neutral, and negative response; stimulation of the more excitable side will give only the positive. The question as to which side is the more excitable can easily be determined by applying to the organ a diffuse electric shock. The more contracted and concave side is the more excitable.

I may now classify some of the principal types of response that will be met in practice. In anisotropic organs, stimulus is supposed to be applied on the less excitable side.

I. Radial organ—

- (a) Thick stem, transverse conduction negligible: positive phototropic response.
- (b) Thin stem, transverse conduction possible: sequence of responses—positive, neutral, and negative.

II. Pulvinated organ, motile or non-motile—

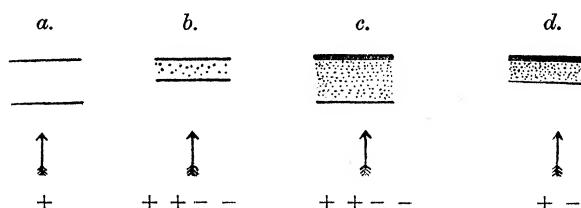
(a) Transverse conduction negligible: positive response; pronounced concavity of the excited side, *e.g.*, mid-day sleep or paraphototropism of *Erythrina indica*, *Clitoria ternatea*, and others.

(b) Transverse conduction moderate: sequence of response positive, neutral, and negative, *e.g.*, main pulvinus of *Mimosa*.

(c) Pulvinus thin and transverse conduction pronounced: transient and hitherto unnoticed positive followed by predominant negative; application of stimulus on the opposite and more excitable side produces movement in the same direction, now positive response. The result would thus appear to be independent of the direction of light. Examples are found in the photonastic movements of lateral leaflets of *Mimosa pudica* and leaflets of *Biophytum sensitivum*.

The following is a diagrammatic representation of the typical cases:—

(Arrow represents direction of incident light.)



- (a) Radial thick organ. Transverse conduction absent. Response positive.
- (b) Radial thin organ. Presence of dots represents possibility of transverse conduction. Sequence of response: positive, neutral, and negative.
- (c) Anisotropic thick organ. Thick line represents the more excitable opposite side. Sequence of response: positive, neutral, and pronounced negative.
- (d) Anisotropic thin organ. High transverse conductivity. Sequence of response: positive, quickly masked by negative.

When light strikes on the opposite side, the sign of response in (a) and (b) will remain unchanged. In (c) and (d) the effect will be only positive.

The demonstration of these different growth-reactions is given in the following series of experiments.

15. *Dia-phototropism and Negative Phototropism.*

Oltmanns found that the seedling of *Lepidium sativum* assumed a transverse or dia-heliotropic position under intense and long-continued action of light of 600,000 Hefner lamps. He regards the transverse as the indifferent position. In reality it is the expression of balanced neutralisation caused by transversely conducted excitation. I obtained such neutralisation with prolonged unilateral exposure to arc-light. The first effect was positive. This was gradually neutralised under continued exposure for two hours; even then the neutralisation was not complete.

Expt. 13.—From the theoretical considerations that have been advanced it would appear that a reversal can only take place under intense light and where there is a possibility of conduction in a transverse direction. Acting on this idea, I employed light from a mercury-vapour lamp, which emits the most effective violet and ultra-violet rays. The specimen was a thin seedling of the rice plant, *Oryza sativa*. The first effect was a positive curvature; this was neutralised and reversed with increasing transverse conduction. The neutralisation was completed in six minutes. The response was afterwards reversed to pronounced negative* by the continued action of light (fig. 15, a).

There is a difficulty in connection with the reversal of response which cannot be explained by mere conduction of excitation to the opposite side, for in a radial organ the contraction of the distal side due to transverse conduction of excitation cannot be greater than that of the directly excited proximal side. The only explanation that remains is that a relaxation takes place on the

* For explanation of negative phototropism of certain roots *cf.* 'Plant Response,' p. 601.

proximal side by the direct action of intense and long-continued stimulation. The following experiment was undertaken to decide the question.

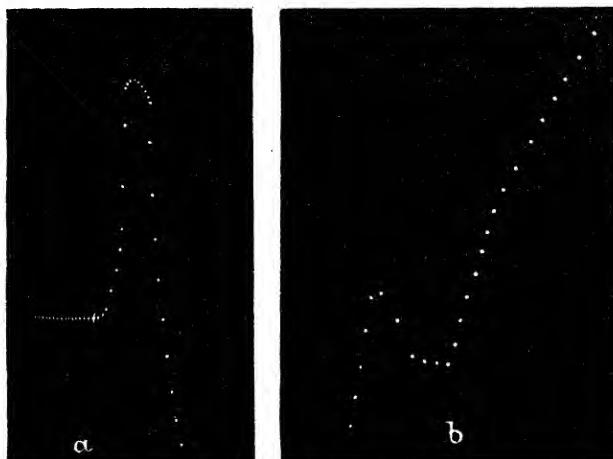


FIG. 15.—*a*, positive, dia-, and negative phototropic response of *Oryza* under continued unilateral stimulus of intense light from arc-lamp; *b*, record on moving plate of modification of growth under continued stimulation of ultra-violet from mercury-vapour lamp. Application of light at thick dot. Note arrest of growth, contraction and subsequent renewal of growth.

Expt. 14. Reversal of normal Retardation of Growth under prolonged Stimulation.—I took a seedling of *Oryza* and by means of inclined mirrors applied light from a mercury-vapour lamp to act on all sides of the organ. The record (fig. 15, *b*) shows that after the normal contraction and retardation a reversal took place, resulting in expansion. The result is not unlike the contraction of muscle passing into relaxation under continuous stimulation. The first effect of stimulation was an arrest of growth and pronounced contraction, but afterwards growth became renewed. It will thus be seen that while under normal circumstances growth is retarded or arrested by light, under prolonged illumination the organ may sometimes recover itself from the state of arrested growth.

16. Radio-thermotropism.

Expt. 15.—I have explained (Section 13) that rise of temperature and radiation of heat induce opposite physiological effects. In the thermonastic reaction of the *Crocus* flower, rise of temperature induces an acceleration of growth, but radiant heat causes a retardation (*cf.* Expt. 10). The tropic effect of thermal rays is as strong, if not stronger, than that induced by the effective blue rays in the spectrum. This will be seen in the following record,

obtained in the stem of *Dregea volubilis*, where successive short exposures to thermal rays from a platinum spiral gave positive responses followed by recovery. Continuous exposure gave all the different phases of maximum positive, neutralisation, and reversal into negative (fig. 16), just as under violet and ultra-violet rays from the mercury lamp. The reversal into

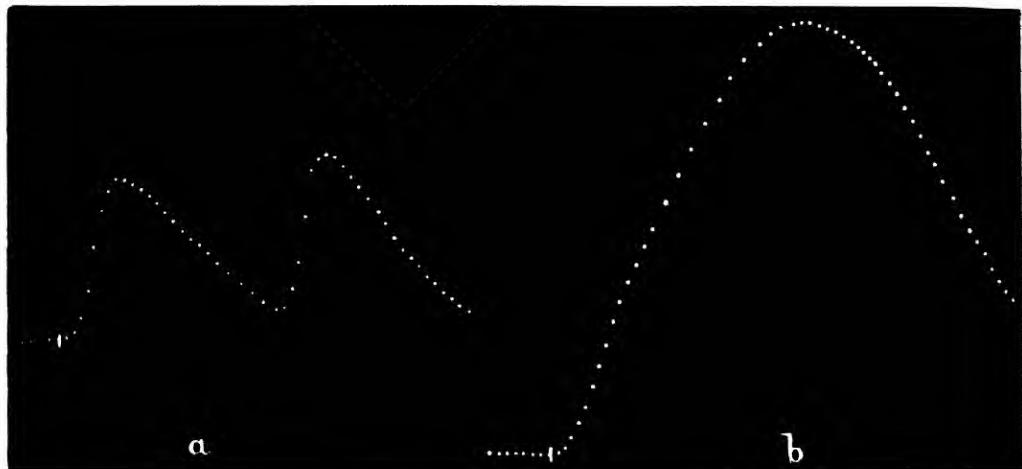


FIG. 16.—*a*, positive responses to short exposure to thermal radiation; *b*, positive, neutral, and reversed negative under continued action of radiation. The negative response went off the plate. Successive dots at intervals of 5 seconds.

negative took place within the comparatively short period of 7 minutes. It will thus be seen that, in inducing phototropic curvature, the heat-rays in sunlight play as important a part as the more refrangible rays of the spectrum.

17. Photonasty.

The leaflets of *Mimosa pudica*, as has been stated before, fold themselves upwards when strongly illuminated either from above or below. Under similar circumstances the leaflets of *Biophytum sensitivum* and *Averrhoa* fold downwards. Diffuse stimulation by electric shock brings about upward closure of leaflets of *Mimosa*, and downward closure of those of *Biophytum* and *Averrhoa*. The excitability of the pulvinule is thus greater on the upper side in *Mimosa* and on the lower side of *Biophytum* and *Averrhoa*.

Expt. 16.—I constructed a very delicate lever, with very little weight, in order to obtain a record of the response of the minute leaflets. Light of moderate intensity from an incandescent lamp was applied on the less excitable side of the pulvinule, that is to say, on the lower side of *Mimosa* and the upper side of *Averrhoa* leaflets. The results show that the immediate

response was in both cases positively phototropic, *i.e.*, a movement towards the source of illumination. This effect was subsequently reversed to strong negative by transverse conduction (fig. 17). Had a delicate means of record

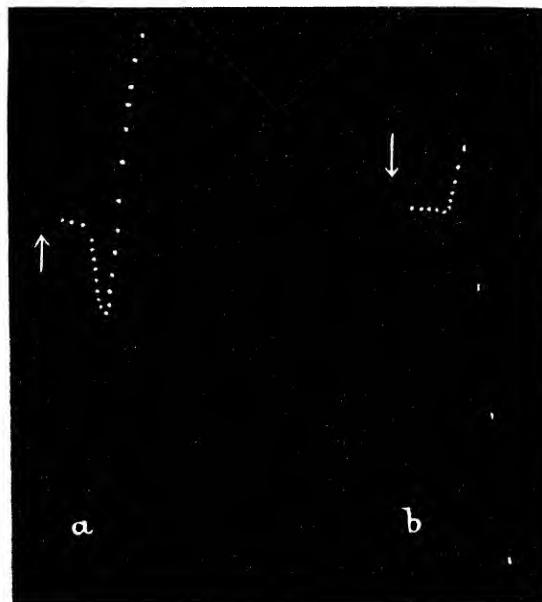


FIG. 17.—Photonastic response : *a*, effect of light applied below on *Mimosa* leaflet; preliminary down or positive movement followed by strong negative up movement. *b*, effect of light applied above on *Averrhoa* leaflet; preliminary up or positive movement followed by pronounced down or negative movement. It is to be noted that movement towards source of illumination is positive. Later and more pronounced negative movement is due to transmitted excitation to the more excitable half of the pulvinule. (Up-movement represented by up-curve and *vice versa*.)

not been available, the gradual transition from positive to negative phototropic curvature would have passed unnoticed. A continuity is thus established between tropic and nastic reactions, rendering the assumption of specific sensibility for each class of phenomena quite unnecessary.

The following laws express the movements of plants under external stimuli and are of universal application :—

1. All forms of stimuli induce contraction as their direct and expansion as their indirect effect.
2. Unilateral stimulation causes positive curvature by contraction of the proximal and expansion of the opposite side.
3. Transverse conduction of excitation induces contraction of opposite side, neutralising or reversing the positive responsive curvature.

4. These effects are accentuated by the differential excitabilities of the two halves of an anisotropic organ.

D. RELATION BETWEEN RESPONSE TO STIMULATION OF GROWING AND OF NON-GROWING ORGANS.

18. *Similarity of Response of Growing and of Non-growing Organs.*

I have throughout this paper adduced numerous instances of the essential similarity between the response of motile and that of growing organs. The following tabular statement will show that a fundamental reaction finds expression in diverse ways, according to different methods of recording response in motile, non-motile, and growing organs:—

Table IV.—Mechanical and Electrical Responses in Motile, Non-motile and Growing Organs.

Inducing cause.	Change of form.	Mechanical response.	Electrical response.
Direct stimulation	Contraction	Fall of leaf ; negative response	Negative response.
Indirect stimulation	Expansion	Erection of leaf ; positive response	Positive response.
Effect of increasing turgor	Expansion	Erection of leaf ; positive response	Positive response.

It has been shown that any agent which increases the excitability of pulvinate organs, as measured by the amplitude of response, mechanical or electrical, likewise induces a positive variation or enhancement of the rate of growth. Conversely, a depressor which brings about a diminution in the amplitude of their mechanical and electrical response also causes depression in the normal rate of growth.

The tropic effect of light is the same on growing as on motile organs. The particular rays which are effective in one case are also effective in the other. Red and yellow rays are ineffective in both. In one case, as in others, we obtain the positive, the dia-positive, and the negative. The tropic movements are determined in both by the same combination of the effects of direct and indirect stimulation.

Owing to the varying combinations of effects of numerous unknown factors the phenomenon of growth presents many perplexities. We may take, for example, the case of the action of external stimulus on growth. Here sub-minimal stimulus induces one effect and moderate stimulus the very opposite.

Should the tonic condition of the plant happen to be below par, the effect of stimulus will be an abnormal acceleration of growth, but during the course of the experiment (owing to the continued action of stimulus) the effect will mysteriously revert to the normal retardation. The point of application of stimulus will introduce further complication, indirect stimulation inducing an effect precisely the opposite to that of direct application. The response under unilateral stimulation is further modified by transverse conductivity, by the intensity of stimulation, and the differential excitability of the organ. In an actual experiment the permutation and combination of these different factors will give rise to effects which will, no doubt, appear as highly capricious. These complexities have led Pfeffer to state that an empirical treatment of the subject of growth is all that is possible in the present state of our knowledge. He, however, adds that "deductive treatment still remains the ideal of physiology, and only when this ideal has been attained shall we be able to obtain a comprehensive view of the interacting factors at work in the living organism."*

I have attempted in the present paper to contribute towards a deductive treatment of the subject by investigating the isolated effect of each of the numerous complicating factors.

Among these, we have the changing influence of the environment, which cannot be kept strictly constant for more than a short time. Besides this, "there are the numerous and varied stimulating and mechanical interactions between different organs." The changing influence of the environment can in practice be eliminated by reducing the period of experiment to a very short time (rendered possible by the employment of the high magnification crescograph) and studying the influence of one factor at a time. Shortening the period of experiment also excludes the interaction of distant organs, for its influence can only be exerted after a certain lapse of time. The organ to be experimented on can thus be isolated from the influence of changing environment and from the interactions of neighbouring organs. In this state of isolation the response under normal conditions is found to be very definite. A given modification of normal response can, moreover, be traced to the definite variation of effect due to the change in the intensity and point of application of stimulus, or in the tonic condition of the reacting organ.

SUMMARY.

The most important results that I have so far obtained from experiments with the crescograph are briefly as follow:—

1. Under lowering of temperature the growth-rate undergoes a diminution

* Pfeffer, *ibid.*, vol. 2, p. 1.

and arrest at a definite temperature. In *Scirpus Kysoor* the arrest takes place at 22° C. Rise of temperature enhances the rate of growth to an optimum, beyond which there is a decline. At 60° C. a violent contraction takes place, which is the spasm of death.

2. Heat induces two effects, which are diametrically opposite to each other. The thermal effect of heat is to increase the rate of growth; the radiation effect is a retardation.

3. The closest parallelism has been established between the response to stimulation given by pulvinate and by growing organs respectively. Conditions which give rise to negative mechanical or electric response of the former also give rise to negative variation or retardation of growth. This is also true of positive mechanical or electric response and positive variation or enhancement of growth. The physiological machinery is the same in pulvinate and non-pulvinate, in growing and non-growing organs.

4. Every stimulus is shown to give rise to two distinct impulses: a hydro-positive, independent of the conductivity of the tissue, and an excitatory negative, which is dependent on the conducting power. The former is transmitted quickly; the latter, being a phenomenon of conduction of protoplasmic change, is propagated slowly. The hydro-positive impulse gives rise to expansion, the excitatory negative to contraction. The transverse conductivity of an organ is very much less than its longitudinal conductivity.

5. Investigation on the effect induced by all forms of stimuli has led to the establishment of the following law: *Direct application of stimulus induces contraction; indirect application gives rise to expansion.*

Direct stimulation of the responding region causes a contractile fall of the motile leaf, or a retardation of growth in a growing organ. The transmitted or indirect effect of stimulus applied at a distance is to induce an erection of the leaf and an acceleration of the rate of growth.

6. This latter fact may offer an explanation of the opposite effects of the stimulus of gravity on root and shoot. In the root, the stimulus is received at the tip, and transmitted to the distant region of growth. Stimulation here is indirect. In the shoot, stimulation is direct, since the growing region of the shoot is both sensitive and responsive. The opposite signs of response in shoot and root may, therefore, be due to the fact that in one case the stimulation is direct and in the other indirect.

7. Tropic movements also are subject to the laws of direct and indirect stimulation. The directly excited proximal side undergoes contraction, the opposite side undergoes expansion; both these factors conspire to induce a positive curvature. This fundamental effect undergoes modification on account of transverse conduction of excitation bringing about neutralisation

or reversal. This may become accentuated by differential excitability of the two sides of the organ.

8. The normal effect undergoes modification when the tissue is in the condition of sub-tonicity. The effect of stimulus on a sub-tonic pulvinus is a positive mechanical or positive electrical response ; corresponding to this is the positive variation or acceleration of growth in sub-tonic tissues, under the stimulus of light or of electric shock. Continuous stimulation converts abnormal positive to normal negative.

9. Mechanical friction induces retardation of growth ; wounds cause a more pronounced and persistent retardation. Unilateral stimulation of contact brings about positive curvature in a tendril by the retardation of growth at the proximal and acceleration at the opposite side.

10. Electric stimulus induces retardation. Growth is affected by an intensity of electric shock which is far below human perception ; the latent period diminishes with increasing intensity of stimulus from 6 seconds to less than a second. The incipient contraction under feeble stimulus culminates under strong stimulus to a marked contraction of the growing organ. The response of the growing organ is similar to the response of pulvinate organs. In the polar action of electric current on growth, the anode is found to enhance and the cathode to depress the normal rate. Unilateral stimulation causes a positive phototropic curvature.

11. Light causes retardation of growth ; intense illumination arrests growth ; but under long-continued exposure, growth may become renewed. Unilateral application of increasing intensity causes a positive, dia-phototropic, and reversed negative response. The more refrangible rays are the more effective, the ultra-violet being most so. The thermal rays in the infra-red are also effective. The phototropic curvature under sunlight is partially due to the obscure radiation.

12. These phototropic effects are accentuated in anisotropic organs where one side is more excitable than the other. Tropic and nastic movements are not distinct phenomena, but a continuity exists between the two.

13. From the above it will appear that the generalisation has been reached—that all the induced movements of plants under environmental changes are the definite effects of direct and indirect stimulation.

I take this opportunity to express my acknowledgment to Mr. P. C. Lyon, C.S.I., the retired Minister in charge of Education to the Government of Bengal, for the facilities afforded to me and for his unremitting interest in research.

I also wish to offer my special thanks to the Royal Society which has not

only extended the hospitality of publication to me for the last 22 years, but has also afforded me assistance from the Government Grant placed at its disposal.

It is now my good fortune to have been able to found a Research Institute, from which the present paper forms the first instalment of work. It is my wish that the facilities of this Institute should be available to research workers from all countries. In this I am attempting to carry out the tradition of my country, which, so far back as 25 centuries ago, welcomed scholars from all parts of the world within the precincts of its ancient seats of learning at Nalanda and at Taxilla.

*Investigations dealing with the State of Aggregation. Part IV.—
The Flocculation of Colloids by Salts containing Univalent
Organic Ions.*

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(Communicated by V. H. Blackman, F.R.S. Received June 18, 1918.)

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Theory and Scope of the Researches.

In an earlier paper* the action of salts in a heterogeneous system was discussed, and the factors which exert influence on the state of hydration and aggregation of the "colloid phase" were summarised. The present communication deals with only one of these factors, *viz.*, the surface-tension of the solutions and the relationship between this property and the capacity of salts for flocculating colloids.

The mechanism by means of which this flocculation is produced is still a matter of considerable controversy. The view which appears, up to the present, to be most widely maintained is that the precipitation depends, in the first instance, on the adsorption of the active (precipitating) ion by the colloid. According to Freundlich, who is mainly responsible for what may be termed the adsorption hypothesis,† the action of the ions can be explained

* Schryver and Hewlett, 'Roy. Soc. Proc.,' B, vol. 89, p. 361 (1916). For Parts I-III of this series see 'Roy. Soc. Proc.,' B, vol. 83, pp. 96, 113, 119 (1910).

† Freundlich, 'Zeitsch. Physikal. Chem.,' vol. 73, p. 385 (1910); Freundlich and Gann, 'Kolloid-chem. Beihefte,' vol. 8, p. 108 (1916).